

The Neuroscience of Language

On Brain Circuits of Words
and Serial Order

FRIEDEMANN PULVERMÜLLER

Cognition and Brain Sciences Unit
Medical Research Council



CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa
<http://www.cambridge.org>

© Cambridge University Press 2002

This book is in copyright. Subject to statutory exception
and to the provisions of relevant collective licensing agreements,
no reproduction of any part may take place without
the written permission of Cambridge University Press.

First published 2002

Printed in the United Kingdom at the University Press, Cambridge

Typefaces Times Ten 10/12.5 pt. and Avenir *System* L^AT_EX 2_ε [TB]

A catalog record for this book is available from the British Library.

Library of Congress Cataloging in Publication Data

Pulvermüller, Friedemann.

The neuroscience of language : on brain circuits of words and serial
order / Friedemann Pulvermüller.

p. ; cm.

Includes bibliographical references and index.

ISBN 0-521-79026-3 (hardback) – ISBN 0-521-79374-2 (pbk.)

1. Neurolinguistics. 2. Speech. 3. Neural networks (Neurobiology) I. Title.
[DNLM: 1. Brain – physiology. 2. Language. 3. Cognition. WL 300 P983n 2002]

QP399. P856 2002

612.7'8 – dc21

2002019360

ISBN 0 521 79026 3 hardback

ISBN 0 521 79374 2 paperback

Contents

<i>Preface</i>	<i>page xi</i>
1 A Guide to the Book	1
1.1 Structure and Function of the Book	1
1.2 Paths Through the Book	2
1.3 Chapter Overview	4
1.3.1 Chapter 1: A Guide to the Book	4
1.3.2 Chapter 2: Neuronal Structure and Function	4
1.3.3 Chapter 3: From Aphasia Research to Neuroimaging	4
1.3.4 Chapter 4: Words in the Brain	4
1.3.5 Excursus E1: Explaining Neuropsychological Double Dissociations	5
1.3.6 Chapter 5: Regulation, Overlap, and Web Tails	5
1.3.7 Chapter 6: Neural Algorithms and Neural Networks	5
1.3.8 Chapter 7: Basic Syntax	5
1.3.9 Chapter 8: Synfire Chains as the Basis of Serial Order in the Brain	6
1.3.10 Chapter 9: Sequence Detectors	6
1.3.11 Chapter 10: Neuronal Grammar	6
1.3.12 Chapter 11: Neuronal Grammar and Algorithms	6
1.3.13 Excursus E2: Basic Bits of Neuronal Grammar	7
1.3.14 Excursus E3: A Web Response to a Sentence	7
1.3.15 Chapter 12: Refining Neuronal Grammar	7
1.3.16 Excursus E4: Multiple Reverberation for Resolving Lexical Ambiguity	7
1.3.17 Excursus E5: Multiple Reverberations and Multiple Center Embeddings	7
	v

1.3.18 Chapter 13: Neurophysiology of Syntax	8
1.3.19 Chapter 14: Linguistics and the Brain	8
2 Neuronal Structure and Function	9
2.1 Neuronal Structure	10
2.1.1 Anatomy of a Nerve Cell	10
2.1.2 Basics of the Cortex	13
2.1.3 Internal Wiring of the Cortex	16
2.2 Neuronal Function and Learning	18
2.3 Principles and Implications	20
2.4 Functional Webs in the Cortex	22
2.4.1 Why Numerous Neurons Should Cooperate	22
2.4.2 The Need for Connecting Neurons in Distant Cortical Areas	23
2.5 Defining Functional Webs	24
2.6 Evidence for Functional Webs	26
2.7 A View of Cortical Function	28
2.8 Temporal Dynamics in Functional Webs: Ignition and Reverberation	29
3 From Classic Aphasia Research to Modern Neuroimaging	33
3.1 Aphasiology	33
3.2 Laterality of Language	39
3.3 Neuroimaging of Language	44
3.4 Summary	48
4 Words in the Brain	50
4.1 Word-Form Webs	50
4.2 Category-Specific Word Webs	56
4.2.1 Visually Related and Action Words	56
4.2.2 Sub-types of Action Words	62
4.3 The Time Course of Lexical and Semantic Activation	62
4.4 Summary and Conclusions	64
Excursus E1: Explaining Neuropsychological Double Dissociations	66
E1.1 Functional Changes in a Lesioned Network: The Nonlinear Deterioration of Performance with Growing Lesion Size	67
E1.2 Broca's vs. Wernicke's Aphasias	69

5 Regulation, Overlap, and Web Tails	74
5.1 Regulation of Cortical Activity	75
5.1.1 The Overactivation Problem in Autoassociative Memories	75
5.1.2 Coincidence vs. Correlation	76
5.1.3 Sparse Coding	76
5.1.4 A Cybernetic Model of Feedback Regulation of Cortical Activity	78
5.1.5 Striatal Regulation of Cortical Activity	80
5.1.6 Summary	81
5.2 Overlapping Representations	82
5.2.1 Homophones and Form-Related Words	83
5.2.2 Synonyms	87
5.2.3 Prototypes and Family Resemblance	88
5.3 Web Tails	91
5.3.1 Affective and Emotional Meaning	91
5.3.2 Linking Phonological, Orthographical, and Meaning-Related Information	91
5.4 Summary	95
6 Neural Algorithms and Neural Networks	96
6.1 McCulloch and Pitts's Logical Calculus as a Starting Point	97
6.2 Symbolic Connectionist Models of Language	107
6.3 Distributed Connectionist Models of Language	112
6.4 Hot Topics in Neural Network Research on Language	115
6.4.1 Word Category Deficits	115
6.4.2 The Development of Rules in the Brain	119
7 Basic Syntax	124
7.1 Rewriting Rules	125
7.2 Center Embedding	128
7.3 Discontinuous Constituents and Distributed Words	134
7.4 Defining Word Categories in Terms of Complements: Dependency Syntax	139
7.5 Syntactic Trees	141
7.6 Questions for a Neuronal Grammar	144
8 Synfire Chains as the Basis of Serial Order in the Brain	147
8.1 Neurophysiological Evidence and Neuronal Models	147
8.2 A Putative Basis of Phonological Processing	151
8.3 Can Synfire Chains Realize Grammar?	154
8.4 Functional Webs Composed of Synfire Chains	156
8.5 Summary	158

9 Sequence Detectors	159
9.1 Movement Detection	159
9.2 Sequence Detectors for Word Strings	161
9.3 Sequence Detectors and Syntactic Structure	163
10 Neuronal Grammar	168
10.1 The Story So Far	169
10.2 Neuronal Sets	169
10.3 Threshold Control	175
10.4 Sequence Detection in Networks of Neuronal Sets	177
10.5 Activity Dynamics of Sequence Detection	181
10.6 Lexical Categories Represented in Neuronal Sets	186
10.6.1 Why Lexical Categories?	186
10.6.2 Lexical Ambiguity	187
10.6.3 Lexical Categories as Sets of Sequence Sets	190
10.6.4 Neuronal Requirements of a Grammar Machine	192
10.6.5 Lexical Disambiguation by Sequence Sets	194
10.7 Summary: Principles of Neuronal Grammar	200
11 Neuronal Grammar and Algorithms	207
11.1 Regular Associations, Associative Rules	207
11.2 A Formalism for Grammar Networks	209
11.3 Some Differences Between Abstract and Neuronal Grammar	211
11.4 Summary	214
Excursus E2: Basic Bits of Neuronal Grammar	215
E2.1 Examples, Algorithms, and Networks	215
E2.2 Grammar Circuits at Work	217
E2.2.1 Simulation 1: Acceptance of a Congruent String	219
E2.2.2 Simulation 2: Processing of an Incongruent String	220
E2.2.3 Simulation 3: Processing of a Partly Congruent String	222
Excursus E3: A Web Response to a Sentence	224
E3.1 The Grammar Algorithm and Network	225
E3.2 Sentence Processing in Syntactic Circuits	227
E3.2.1 Global Characteristics	228
E3.2.2 Specific Features	231
E3.3 Discussion of the Implementation and Simulation	232
12 Refining Neuronal Grammar	235
12.1 Complements and Adjuncts	236
12.2 Multiple Activity States of a Neuronal Set	238
12.2.1 The Concept of Multiple Reverberation	239

12.2.2 Some Revised Principles of Neuronal Grammar	241
12.3 Multiple Center Embedding	245
12.4 Summary, Open Questions, and Outlook	247
Excursus E4: Multiple Reverberation for Resolving Lexical Ambiguity	250
Excursus E5: Multiple Reverberations and Multiple Center Embeddings	255
13 Neurophysiology of Syntax	265
13.1 Making Predictions	265
13.2 Neuronal Grammar and Syntax-Related Brain Potentials	266
14 Linguistics and the Brain	270
14.1 Why Are Linguistic Theories Abstract?	270
14.2 How May Linguistic Theory Profit from a Brain Basis?	272
<i>References</i>	277
<i>Abbreviations</i>	297
<i>Author Index</i>	301
<i>Subject Index</i>	307

A Guide to the Book

The neuroscience of language is a multidisciplinary field. The reader's primary interest may therefore lie in various classical disciplines, including psychology, neuroscience, neurology, linguistics, computational modeling, or even philosophy. Because readers with different backgrounds may be interested in different parts of this book, Chapter 1, Section 1.3 gives an overview of the book contents and the gist of each chapter. In Section 1.1, the general structure of the book is explained; subsequently, paths through the book are recommended for readers with different backgrounds and interests in Section 1.2.

1.1 Structure and Function of the Book

The fourteen chapters of this book are mainly designed to convey one single message: It is a good idea to think about language in terms of brain mechanisms – to spell out language in the language of neurons, so to speak. Making this point is not a new proposal. One can find similar statements in classical writings; for example, in Freud's monograph on aphasia (Freud, 1891) and other publications by neurologists in the late nineteenth century, and, of course, in modern brain-theoretical and linguistic publications (Braitenberg, 1980; Mesulam, 1990; Schnelle, 1996a). However, a systematic model of language at the level of neurons as to date is not available, at least, not an approach that would be both grounded in empirical research while at the same time attacking a wide range of complex linguistic phenomena.

Apart from the main message, this book puts forward two principle proposals: First, that words are represented and processed in the brain by strongly connected distributed neuron populations exhibiting specific topographies. These neuron ensembles are called *word webs*. Second, that

grammar mechanisms in the brain can be thought of in terms of neuronal assemblies whose activity specifically relates to the serial activation of pairs of other neuron ensembles. These assemblies are called *sequence sets*. The proposal about word webs is presented in Chapter 4 and the one about sequence sets in Chapter 10. One may therefore consider Chapters 4 and 10 the core chapters of this book.

As it happens, new proposals elicit discussion, which, in turn, makes refinement of the original proposals desirable. The word web proposal is being refined in Chapters 5 and 8, and the proposal on grammar mechanisms is further developed in Chapters 11 and 12. As stressed in the Preface, several colleagues contributed to the refinements offered. The evolution of some of the ideas is documented in a recent discussion in the journal *The Behavioral and Brain Sciences* (Pulvermüller, 1999b). Summaries of ideas put forward here can be found in related review papers (Pulvermüller, 2001, 2002).

Apart from presenting the two main proposals, the book is designed to give the reader an introduction to basic knowledge from disciplines relevant in the cognitive neuroscience of language. Chapter 2 offers an introduction to neuroscience and cognitive brain processes. Chapter 3 introduces basics about classical aphasia research and modern neuroimaging of language. Two more introductory chapters follow approximately in the middle of the book. Chapter 6 features neural network approaches to language, and Chapter 7 introduces basics of syntactic theories. These introductory chapters were written to make the book “self-contained,” so that ideally speaking no prior special knowledge would be required to understand it.

Interspersed between the chapters are five excursions, labeled E1 through E5, which illustrate the functioning of brain models of language. In each excursion, one or more simple simulations are summarized that address an issue raised in the preceding chapter. Computer simulations of the main syndromes of aphasia (Excursus E1) are included along with simulations of the processing of simple (Excursus E2) and gradually more complex (Excursuses E3–E5) sentences in brain models of grammar. Some of the simulations are available as animations accessible through the Internet.

1.2 Paths Through the Book

Clearly, the reader can choose to read through the book from beginning to end. However, because not all issues covered by the book may be in the inner circle of one’s personal “hot topics,” it may be advantageous to have available alternatives to this global strategy. One alternative would be to take a glance at the main chapters (4 and 10) or at the introductory chapter concerning the topic one is particularly keen on. However, one may

Table 1.1. Routes through the book recommended to readers primarily interested in neuroscience, linguistics, or neuronal modeling, respectively. Chapter numbers and headings are indicated. Headings are sometimes abbreviated. Excursuses are referred to by the letter E plus a number and by abbreviated headings. For further explanation, see text.

Neuroscience Route	Linguistics Route	Modeling Route
2 Neuronal structure and function	4 Words in the brain	4 Words in the brain
3 Aphasia and neuroimaging	7 Basic syntax	5 Regulation, overlap, web tails
4 Words in the brain	8 Synfire chains	6 Neural networks
E1 Double dissociations	9 Sequence detectors	E1 Double dissociations
5 Regulation, overlap, web tails	10 Neuronal grammar	E2 Basic bits of neuronal grammar
8 Synfire chains	11 Neuronal grammar and algorithms	E3 Web response to a sentence
9 Sequence detectors	12 Refining neuronal grammar	E4 Lexical ambiguity
13 Neurophysiology of syntax	14 Linguistics and the brain	E5 Center embedding

wish to dive deeper into the matter while still primarily following one’s interests.

For this latter purpose, three paths through the book are offered for a reader primarily interested in neuroscience, linguistics, and neurocomputational modeling. If one chooses one of these options, one should be aware that the routes are not self-contained and consultation of other chapters may be relevant occasionally. To facilitate detection of relevant information in other chapters of the book, multiple cross-references have been added throughout.

The three paths through the book are presented in Table 1.1. Please consult the overview, Section 1.3, for details about chapter contents.

It is difficult to decide what to recommend to a reader primarily interested in psychology. Because psychology is a rather wide field, the best recommendation may depend primarily on the subdiscipline of interest. Readers interested in neuropsychology and psychophysiology can be recommended to follow the neuroscience route, whereas those interested in cognitive psychology may tend more toward modeling aspects. The neuroscience route would also be recommended to the reader focusing on neuroimaging or neurology. A philosopher may be most interested in the open questions that accumulate in Chapters 5, 12, and 14.

1.3 Chapter Overview

1.3.1 Chapter 1: A Guide to the Book

The main purpose of the book and its structure are explained briefly. Recommendations are given concerning how to use the book if one is interested primarily in its neuroscience, linguistics, or modeling aspects. The gist of each book chapter is summarized briefly.

1.3.2 Chapter 2: Neuronal Structure and Function

Chapter 2 introduces basics about the anatomy and function of the neuron and the cortex. Principles of cortical structure and function are proposed that may be used as a guideline in cognitive brain research. The concept of a distributed functional system of nerve cells, called *functional web*, is introduced and discussed in the light of neurophysiological evidence.

1.3.3 Chapter 3: From Aphasia Research to Neuroimaging

Basics about *aphasias*, language disorders caused by disease of the adult brain, are summarized. Aphasia types and possibilities on explaining some of their aspects are being discussed. The issue of the laterality of language to the dominant hemisphere – usually the left hemisphere – is mentioned, and theories of laterality and interhemispheric interaction are covered. Basic insights in the functional architecture of the cortex as revealed by modern neuroimaging techniques are also in the focus. The conclusion is that some, but not all, insights from classical aphasia research about the localization of cortical language functions can be confirmed by neuroimaging research. However, language processes seem to be much more widely distributed than previously assumed. The question about the cortical locus of word semantics, as such, has found contradicting answers in recent imaging research.

1.3.4 Chapter 4: Words in the Brain

The proposal that words are cortically represented and processed by distributed functional webs of neurons is elaborated and discussed on the basis of recent neuroimaging studies. The data support the postulate that words and concepts are laid down cortically as distributed neuron webs with different topographies. The strongly connected distributed neuron ensembles representing words are labeled *word webs*. Word webs may consist of a phonological part (mainly housed in the language areas) and a semantic part

(involving other areas as well). For example, processing of words with strong associations to actions and that of words with strong visual associations appears to activate distinct sets of brain areas. Also, different subcategories of action words have been found to elicit differential brain responses. This supports the proposed model.

1.3.5 Excursus E1: Explaining Neuropsychological Double Dissociations

A simulation is presented that allows for the explanation of neuropsychological double dissociations on the basis of distributed functional webs of neurons. The nonlinear decline of performance of the models with lesion size and its putative neurological relevance are also mentioned.

1.3.6 Chapter 5: Regulation, Overlap, and Web Tails

Chapter 5 deals with open issues remaining from earlier chapters. How could a regulation device controlling activity in the cortex be organized? How would words with similar meaning but different form, or words with similar form but different meaning, be realized in the brain? Would the brain's word processor be restricted to the cortex, or can word webs have subcortical "tails"? One postulate is that multiple overlap between cortical representations exists between word representations.

1.3.7 Chapter 6: Neural Algorithms and Neural Networks

An introduction into neural network models is given. McCulloch and Pitt's theory is sketched and perceptron-based simulations are featured. Symbolic connectionist approaches are also discussed briefly. Among the hot topics featured are the explanation of word category deficits as seen in neurological patients and the development of rules in infants' brains.

1.3.8 Chapter 7: Basic Syntax

A few terms and theoretical approaches to syntax are introduced. Phrase structure grammars, dependency grammars, and more modern proposals rooted in these classic approaches are discussed. Syntactic problems such as those associated with long-distance dependencies and center embeddings are mentioned. Chapter 7 ends with a list of issues with which grammar circuits should cope.

1.3.9 Chapter 8: Synfire Chains as the Basis of Serial Order in the Brain

One type of serial-order mechanism in the brain for which there is evidence from neurophysiological research is featured. Called a *synfire chain*, it consists of local groups of cortical neurons connected in sequence, with loops also allowed for (*reverberatory synfire chain*). The synfire model of serial order is found to be useful in modeling phonological–phonetic processes. It is argued, however, that a synfire model of syntax does not appear to be fruitful.

1.3.10 Chapter 9: Sequence Detectors

A second type of serial-order mechanism exists for which there is evidence from brain research. It is the detection of a sequence of neuron activations by a third neuronal element called the *sequence detector*. The evidence for sequence detectors comes from various brain structures in various creatures. It is argued that sequence detectors may operate on sequences of activations of word webs, and that these may be part of the grammar machinery in the brain.

1.3.11 Chapter 10: Neuronal Grammar

Neuronal sets are defined as functional webs with four possible activity states: inactivity (O), full activation or ignition (I), sustained activity or reverberation (R) and neighbor-induced preactivity or priming (P). Reverberation and priming levels can vary. Grammar networks are proposed to be made up of two types of neuronal sets: word webs and sequence sets. Sequence sets respond specifically to word sequences. The lexical category of words and morphemes is represented by a set of sequence sets connected directly to word webs. Words that can be classified as members of different lexical categories have several mutually exclusive sets of sequence sets. Activity dynamics in the network are defined by a set of principles. A grammar network, also called *neuronal grammar*, can accept strings of words or morphemes occurring in the input, including sentences with long-distance dependencies. The hierarchical relationship between sentence parts becomes visible in the activation and deactivation sequence caused by an input string.

1.3.12 Chapter 11: Neuronal Grammar and Algorithms

Three types of formulas are introduced that describe a neuronal grammar network:

1. *Assignment formulas* are definitions of connections between input units and lexical category representations and are analogous to lexicon or assignment rules of traditional grammars.
2. *Valence formulas* are definitions of lexical categories in terms of sequencing units and have some similarity to dependency rules included in dependency grammars.
3. *Sequence formulas* are definitions of connections between sequencing units and have no obvious counterpart in traditional grammars.

1.3.13 Excursus E2: Basic Bits of Neuronal Grammar

Simple word strings are discussed on the basis of grammar networks composed of sequence sets and word webs. How the network accepts a string and how the network behaves if it fails to do so is discussed.

1.3.14 Excursus E3: A Web Response to a Sentence

Processing of an ordinary sentence is simulated in a neuronal grammar architecture. The sentence exhibits six morphemes, subject–verb agreement, a distributed word, and other interesting properties.

1.3.15 Chapter 12: Refining Neuronal Grammar

A revision of the grammar model is proposed that requires stronger assumptions. The core assumption is that neuronal sets exhibit multiple states of reverberation and priming. In the new architecture, the relationship between words and lexical categories is now dynamic.

1.3.16 Excursus E4: Multiple Reverberation for Resolving Lexical Ambiguity

Implementation of multiple lexical category representations of words using mutually exclusive sets of sequence sets allows for modeling sentences in which the same word form is being used twice, as a member of different lexical categories.

1.3.17 Excursus E5: Multiple Reverberations and Multiple Center Embeddings

A network with dynamic binding between word and lexical category representations and the option to activate each neuronal set is introduced on the

background of the machinery discussed in Chapters 10 and 11. This more advanced architecture now models the processing of grammatically complex sentences that include center embeddings.

1.3.18 Chapter 13: Neurophysiology of Syntax

Grammatically incorrect “sentences” elicit specific physiological brain responses. Two such physiological indicators of grammatical deviance are discussed. The neuronal grammar proposal is related to these data, and a putative neurobiological explanation for them is offered.

1.3.19 Chapter 14: Linguistics and the Brain

Linguistics and brain science must merge. This is reemphasized in Chapter 14 where putative advantages of a brain-based language theory are highlighted.